RESIDENCE TIME IN CONCURRENT FORAGING WITH FIXED TIMES TO PREY ARRIVAL

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Five pigeons were trained in a concurrent foraging procedure in which reinforcers were occasionally available after fixed times in two discriminated patches. In Part 1 of the experiment, the fixed times summed to 10 s, and were individually varied between 1 and 9 s over five conditions, with the probability of a reinforcer being delivered at the fixed times always .5. In Part 2, both fixed times were 5 s, and the probabilities of food delivery were varied over conditions, always summing to 1.0. In Parts 3 and 4, one fixed time was kept constant (Part 3, 3 s; Part 4, 7 s) while the other fixed time was varied from 1 s to 15 s. Median residence times in both patches increased with increases in the food-arrival times in either patch, but increased considerably more strongly in the patch in which the arrival time was increased. However, when arrival times were very different in the two patches, residence time in the longer arrival-time patch often decreased. Patch residence also increased with increasing probability of reinforcement, but again tended to fall when one probability was much larger than the other. A detailed analysis of residence times showed that these comprised two distributions, one around a shorter mode that remained constant with changes in arrival times, and one around a longer mode that monotonically increased with increasing arrival time. The frequency of shorter residence times appeared to be controlled by the probability of, and arrival time of, reinforcers in the alternative patch. The frequency of longer residence times was controlled directly by the arrival time of reinforcers in a patch, but not by the probability of reinforcers in a patch. The environmental variables that control both staying in a patch and exiting from a patch need to be understood in the study both of timing processes and of foraging.

Key words: foraging, residence time, choice, reinforcer value, scalar expectancy, key peck, pigeons

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The experimental procedure known as "some patches are empty" was introduced by McNamara and Houston (1985) as a notional procedure that could be used to study some aspects of foraging in the laboratory. In this procedure, following a time that separates successive foraging episodes (travel time), animals enter a patch in which, with some probability, a reinforcer may be available for responding after a variable time in the patch. A second response alternative is also available when the subject is foraging in a patch. If this patch exit response is emitted, the patch ends, a travel time ensues, and another patch begins. With the probabilities of the availability of reinforcers being determined anew on each patch entry, the interesting data are the patch residence times, the times since the start of a patch at which the subject switches out of the patch. McNamara and Houston provided a quantitative model for residence times based on the assumption that subjects optimized the overall rate of reinforcers in the situation. It predicted increases in residence times with increasing times to reinforcers in patches, increasing probabilities of food in patches, and increasing travel times between patches.

Kamil, Misthal, and Stephens (1993) used McNamara and Houston's (1985) procedure with blue jays and reported that their subjects stayed longer in patches before exiting than predicted by McNamara and Houston's maximization theory. These "overstaying" results were replicated with pigeons by Davison and McCarthy (1994) and McCarthy, Voss, and Davison (1994). Jones and Davison (1996) introduced a concurrent variant of the "some patches are empty" procedure in which two discriminated patches were available, with potentially different times to reinforcers (prey-arrival times) and different probabilities of reinforcers in the two patches. Despite the increased complexity of the task, their results closely replicated the results of Kamil et al., Davison and McCarthy, and McCarthy et al.

Brunner, Kacelnik, and Gibbon (1992) reported results from a modified procedure in which up to four prey items could be obtained on a single entry to a patch, each scheduled on equal successive fixed-interval (FI) schedules and terminating in a prey-absent trial. Residence times on prey-absent trials increased with increasing FI values and were reliably longer than the FI schedule value, and deviated further from the FI value as the interval duration was increased. Davison (1996) investigated performance in a similar single ''some patches are empty'' procedure, but used only single reinforcers in each prey patch probabilistically arranged on fixed-time (FT) schedules. Again, residence times were consistently longer than, and increased with increasing, FT arrival times at two different travel times, and residence times also increased with increasing travel time, at least when arrival times were short.

Brunner et al. (1992) provided a theory to explain why subjects stay longer in patches with fixed times to reinforcers than the fixed time at which the reinforcers arrive. They theorized that time spent in a patch was jointly controlled by the subject's memory of times to reinforcers in that patch and by optimization of reinforcer production. Assuming that a subject's memory for arrival times is inaccurate and normally distributed around the actual FT value, maximization of reinforcer frequencies requires that residence times are biased towards longer times than the actual arrival time. This biasing ensures that they remain in the patch sufficiently long on most trials. If they did not do so, then any normal variance in remembered times would result in subjects switching out of the patch before the reinforcer had been obtained on 50% of all trials. The scalar property of time, which is that variance of remembered time intervals increases according to the square of the interval duration, also predicts that as intervals are increased, residence times should increase at a faster rate. This was found by Brunner et al. and by Davison (1996).

In foraging situations in which reinforcers are not obtained upon every entry to a patch, it is likely that the potential for reinforcers in future patches, as well as the arrival times of possible reinforcers in the present patch, may jointly determine when the subject will exit from the patch. If reinforcement for exiting

was unimportant, and thus there was no effect of alternative patch parameters, subjects would surely stay in the one patch forever, or until ejected involuntarily. Brunner et al. (1992) acknowledged that residence times in a patch cannot reflect pure timing processes that are unbiased by reinforcement. They suggested that the criterion for exiting a patch should not be constant, but ''reflects the relative costs of premature and excessive giving-up times. According to this view, the threshold . . . should be chosen so that the net rate of intake is maximum'' (p. 611). Indeed, the finding that increasing travel time between patches increases residence times (Davison & McCarthy, 1994; Kamil et al., 1993; McCarthy et al., 1994) may be understood in terms of an effect of decreasing the reinforcer value of exiting. Specifically, when the times to reinforcer arrivals in patches are held constant, increasing the travel time between patches increases the delay to reinforcers in alternative patches and thus could serve to bias subjects' behavior towards staying longer in the present patch.

These considerations bear on the importance for timing research that measures of timing must be concerned purely with timing and be unaffected by reinforcer values (see Zeiler, 1985). Preston (1994) discussed the degree to which timing in the standard time-left procedure (Gibbon & Church, 1981) is a measure of timing that is unbiased by reinforcement. Preston argued cogently against Gibbon, Church, Fairhurst, and Kacelnik's (1988) argument that, because reinforcer frequencies in the time-left procedure are equal between the choices, unbiased timing measures will be obtained. Indeed, Preston showed that models that do not assume any timing mechanism can predict the results of time-left procedures. Both sets of researchers thus do accept that reinforcer variables affect measures of timing, in general, but they differ sharply as to whether they do or do not in this particular procedure.

The reinforcement approach to performance in timing situations must make the assumption that the point at which a subject exits from one patch—the putative timing point—is the point at which the value of reinforcement on the present alternative changes from being greater than to being less than the value of the other alternative. Fur-

ther, one might presume that if the reinforcers in both patches are temporally distant from this point (as with the timing of long intervals), the local slope of the change in value will be low, producing a wide variance around this point. If reinforcers are temporally close (as with smaller intervals), value-change slopes would likely be higher, and perhaps would produce less variance around the timing point. It is possible, therefore, that the scalar property of temporal control is at least partly produced by the reinforcer values in the situation. The important question may be, then, not whether we can discover a procedure in which timing measures are unaffected by reinforcer variables, but whether we can dissociate reinforcer and timing effects better to understand both of these. The parallel here is in the acceptance in psychophysics that both stimulus discriminability and reinforcer bias play a part in determining what subjects do in the presence of discriminative stimuli, and the need to measure these effects independently (Green & Swets, 1966).

Although they are presumably present, the precise effects of reinforcement for exiting are unclear in the standard "some patches are empty" procedure because the reinforcer parameters of future patches are the same as those arranged in the present patch, so that changes in present- and alternative-patch parameters are confounded. In contrast, the concurrent analogue of this procedure, introduced by Jones and Davison (1996), has the potential to separate the relative contributions to patch residence of both reinforcer-arrival times in the present patch and arrival times following travel in alternative patches. If two patches with different reinforcer-arrival times are signaled by discriminative stimuli and arranged according to the Jones and Davison procedure, residence times in one patch may well be shortened when the arrival time in the alternative patch is made relatively short and be lengthened when the alternative arrival time is made relatively long. For instance, if one arrival time is 1 s and the other is 10 s, with a travel time of 1 s between both, the reinforcement value of exiting the 10-s patch soon after it was entered may be greater than the value of staying for 10 s because a reinforcer in the 1-s patch, if scheduled, is delayed by only 2 s. Also, in the 1-s patch, the value of the reinforcer in the 10-s patch may be sufficiently low so as to delay exiting from this patch until some time after the reinforcer had been due.

The present experiment investigated residence time in a modification of the concurrent "some patches are empty" procedure used by Jones and Davison (1996). The purpose of the present experiment was to investigate more closely timing in patch residence by arranging fixed, rather than variable, times to reinforcers in patches. Either of two patches were available successively in strict alternation on a single key, and each patch was discriminatively signaled by a red or green keylight. A second white key (equivalent to the switching key in Findley, 1958, concurrent scheduling procedures) was also available during patches. A response to this key terminated the current patch and produced a travel time of 1 s in blackout, followed by the start of the alternate patch. Reinforcers in each patch were delivered according to an arranged probability at the end of an FT schedule, that is, without a response being required. This probability was sampled on each patch entry. If a reinforcer was available in a patch on a trial, this was designated a prey trial; otherwise, it was a no-prey trial. All reinforcers in patches were scheduled dependently (Stubbs & Pliskoff, 1969). Using this procedure, four sets of conditions were arranged: First, with prey probabilities of .5 in each patch, we varied the FT schedules in each patch under the constraint that the FTs summed to 10 s. Second, with both FT schedules set to 5 s, we varied the probability of prey in each patch, with the probabilities summing to 1.0. Third, we kept one patch at FT 3 s and varied the other from 1 to 15 s, with both prey-trial probabilities set at .5. Finally, we kept one patch at FT 7 s and varied the other from 1 to 15 s, with prey-trial probabilities again set at .5. These sets of conditions were selected so that we could investigate in detail residence time in one patch in the context of arrival times in the alternate patch. In particular, we wanted to ask how residence times in one patch were affected by arrival times and arrival probabilities in the other patch.

METHOD

Subjects

Five homing pigeons numbered 111 to 113, 115, and 116 were maintained at 85%

±15 g of their ad lib body weights. The subjects were the same as those used by Jones and Davison (1996). The subjects were fed amounts of mixed grain, immediately after sessions, sufficient to maintain their designated body weights.

Apparatus

The apparatus was the same as used by Jones and Davison (1996). All experimental contingencies were arranged on an IBM®-compatible computer, situated remote from the experimental chamber, and running MED-PC® software. The chamber dimensions were 330 mm high, 330 mm wide, and 310 mm deep, and it was fitted with an exhaust fan to provide both ventilation and masking noise. Three 20-mm circular response keys were set 110 mm apart and 250 mm from the grid floor on one wall of the chamber. Only the left and right keys were used in this experiment. The left key was illuminated yellow, and the right key could be illuminated red or green. When lit, the keys were operated by pecks exceeding about 0.1 N. The food magazine was situated beneath the center key and was 120 mm from the floor. During reinforcement, which was 3-s access to wheat throughout, the food hopper was raised and illuminated, and the keylights were extinguished. There was no other source of illumination in the chamber.

Procedure

Because all the subjects had extensive experience on a similar procedure, they required no pretraining and were placed directly on the first experimental condition (Table 1).

Sessions commenced with the right (patch exit or switching) key lit yellow and the left main key lit either red or green randomly. At any time during key illumination, a response to the switching key caused a 1-s blackout of both keys (the travel time) and subsequently alternated the main-key color and patch parameters. It also caused a decision to be made, according to the values of p_{red} and p_{green} (which always summed to 1.0), as to whether a reinforcer was available on this particular entry in the patch switched to. At the start of a session, and after a reinforcer had been obtained from either patch, the patch at which the next reinforcer would be ob-

Table 1

Sequence of experimental conditions, fixed times to reinforcement in the red and green patches, probability of reinforcement in the patches, the part of the experiment to which the condition contributed, and the number of sessins of training given in each condition.

	FT (s)		Probability of reinforcement			Ses-
Condition	Red	Green	Red	Green	Part	sions
1	5	5	.50	.50	1, 2	18
2	7	3	.50	.50	1, 3, 4	20
3	1	9	.50	.50	1	21
4	3	7	.50	.50	1	22
5	9	1	.50	.50	1	19
6	5	5	.75	.25	2	20
7	5	5	.10	.90	2	20
8	5	5	.90	.10	2	21
9	5	5	.25	.75	2	22
10	5	3	.50	.50	3	23
11	7	1	.50	.50	4	21
12	3	3	.50	.50	3	21
13	7	9	.50	.50	4	20
14	7	3	.50	.50	1, 3, 4	19
15	1	3	.50	.50	3	21
16	7	7	.50	.50	4	19
17	9	3	.50	.50	3	20
18	7	5	.50	.50	4	18
19	7	11	.50	.50	4	21
20	11	3	.50	.50	3	20
21	7	15	.50	.50	4	19
22	15	3	.50	.50	3	20

tained was determined probabilistically by $p_{red}/(p_{red} + p_{green})$. In addition, switching into the patch that was allocated a reinforcer determined, according to the values of p_{red} or p_{green}, whether a reinforcer was available on this particular entry to the patch. Thus, a reinforcer might be allocated to a patch but be unavailable on a particular instance of patch residence. This dependent scheduling of reinforcers, along with a reassessment of p_{red} or p_{green} each time a patch was entered, ensured that the ratio of obtained reinforcers did not deviate systematically from that arranged.

On occasions when the patch entered had been allocated a reinforcer, this reinforcer was delivered after a fixed time (FT_{red} or FT_{green}) since patch commencement, provided that the subject remained in the patch for that time. That is, no responding was required to the main key, although the numbers of responses were recorded. If the subject switched before the designated FT had timed out, this reinforcer remained allocated

to this patch but might not be available again on the next entry into that patch. Rather, although the reinforcer remained allocated to the same patch until collected, each time this patch was reentered, p_{red} or p_{green} determined whether a reinforcer was available on the current entry to the patch. After each reinforcer, the travel time ensued, and the subject was then presented with the alternate patch. Sessions ended in blackout after 45 min had elapsed or after 40 reinforcers had been delivered, whichever occurred sooner.

Performance in each condition was judged to be stable when a stability criterion had been met. The first nine sessions of a condition were discarded. From the 10th session on, median green-alternative residence times over three-session blocks were calculated, and the computer searched over successive, overlapping, three-session blocks for the presence or absence of a monotonic trend. When such a trend had not been found on five, not necessarily consecutive, occasions, the subject's performance was taken as stable. Only when this last criterion had been met by all subjects were the experimental conditions changed.

Table 1 shows the sequence of experimental conditions, the parts to which each condition contributed, and the number of sessions to stability. In Part 1, p_{red} and p_{green} were .5 and FT_{red} and FT_{green} summed to 10 s. The value of FT_{red} was varied over conditions from 1 to 9 s in five steps. In Part 2, FT_{red} and FT_{green} were both 5 s and p_{red} and p_{green} summed to 1.0. The value of p_{red} was varied from .1 to .9 over five conditions. In Part 3, the FT_{green} value was 3 s and the value of FT_{red} was varied from 1 to 15 s over seven conditions. Finally, in Part 4, FT_{red} was 7 s and FT_{green} was varied from 1 to 15 s over seven conditions. In Parts 3 and 4, both p_{red} and p_{green} were .5.

The data collected were the numbers of responses emitted on the red and green main keys, the total time spent in each patch, and the number of reinforcers obtained in each patch. In addition, we collected the coded time of every experimental and subject event for later detailed analysis.

RESULTS

The Appendix shows the median of the individual residence times, defined as the times to patch exit on all patch entries that did not terminate in reinforcement, over the last five sessions of each experimental condition for each subject. These data, and more detailed measures of performance over the same sessions, were used in all analyses.

Figure 1 shows median residence times in both patches for each subject as a function of the arrival time of reinforcers in Part 1 when the two fixed times summed to 10 s. There appeared to be no reliable differences between residence times in the two alternatives apart from longer red residence times for Bird 113. In general, replicated points were close to the original points, and to the original data paths, for all subjects except Bird 112. For most subjects, residence times were an increasing function of the arranged arrival times, at least up until one arrival time was between 5 and 7 s (and the other 5 or 3 s). Residence times over this range were consistently longer than arrival times. However, when one arrival time was 9 s (the other 1 s), median residence times on that alternative were considerably shorter than the arrival time in 7 of 10 cases.

In Part 2, the fixed times were both 5 s and the probability of a prey item in each patch was varied under the constraint that the two probabilities summed to 1.0. Figure 2 shows median residence times for each subject in Part 2 as a function of the probability of reinforcers arranged in each patch. As the probability of reinforcement in a patch increased from .1 to .5, residence times increased monotonically for all subjects. However, at probabilities greater than .5, residence times ceased to increase, and even showed some evidence of falling for Birds 111, 112, and 116. In addition, when the probability of reinforcement was .1 in either patch, median residence times were less than the 5-s arrival time in 8 of 10 cases.

Figure 3 shows the median residence times obtained in Part 3 when the reinforcer-arrival time in green was kept at 3 s and the arrival time in red was varied from 1 to 15 s. Replicated conditions again provided data similar to original conditions, except for Bird 112 (the same replication as shown in Figure 1). Red residence times for all subjects increased monotonically as reinforcer-arrival times increased up to an arrival time of 7 s, and beyond this point for Birds 111 and 115. How-
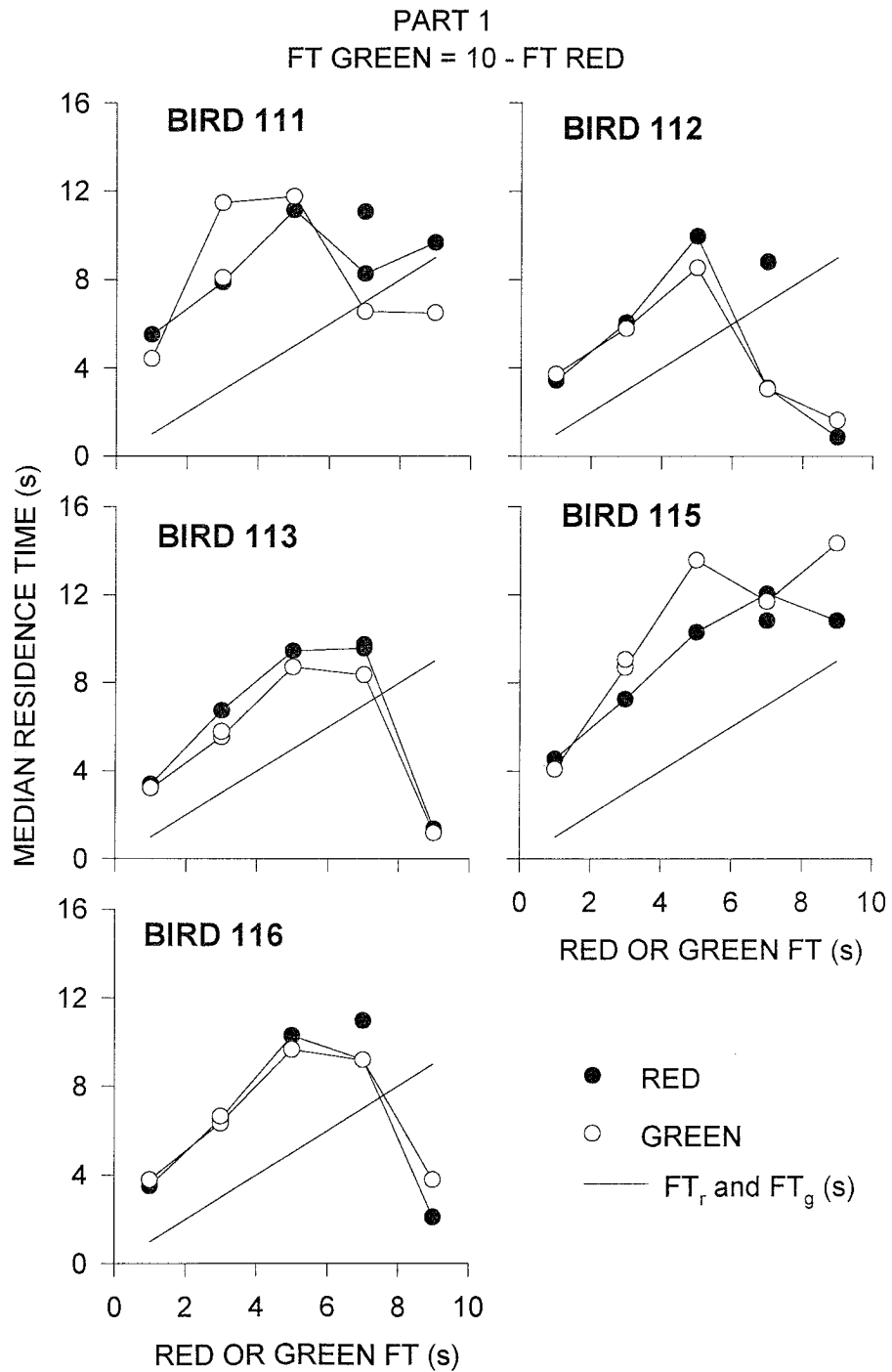
PART 1
FT GREEN = 10 - FT RED

Fig. 1.   Median residence times for all 5 subjects in the red and green patches in Part 1 when red and green FT arrival times summed to 10 s and each was varied from 1 to 9 s. Replications are shown by unjoined points.

PART 2
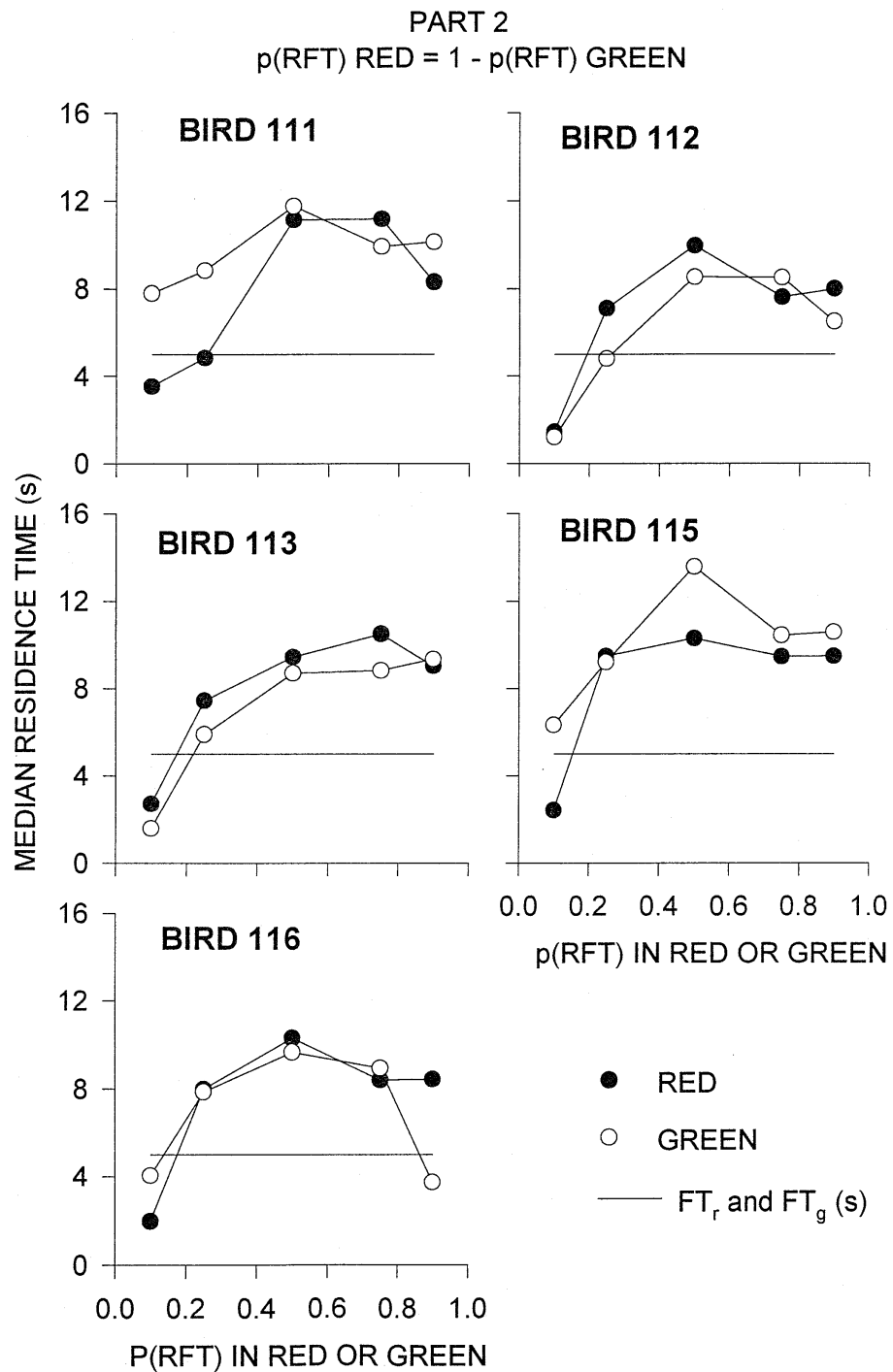## p(RFT) RED = 1 - p(RFT) GREEN

Fig. 2. Median residence times for all 5 subjects in the red and green patches in Part 2 when red and green FT arrival times were both 5 s, the probability of reinforcement in each patch summed to 1.0, and each was varied from .1 to .9.
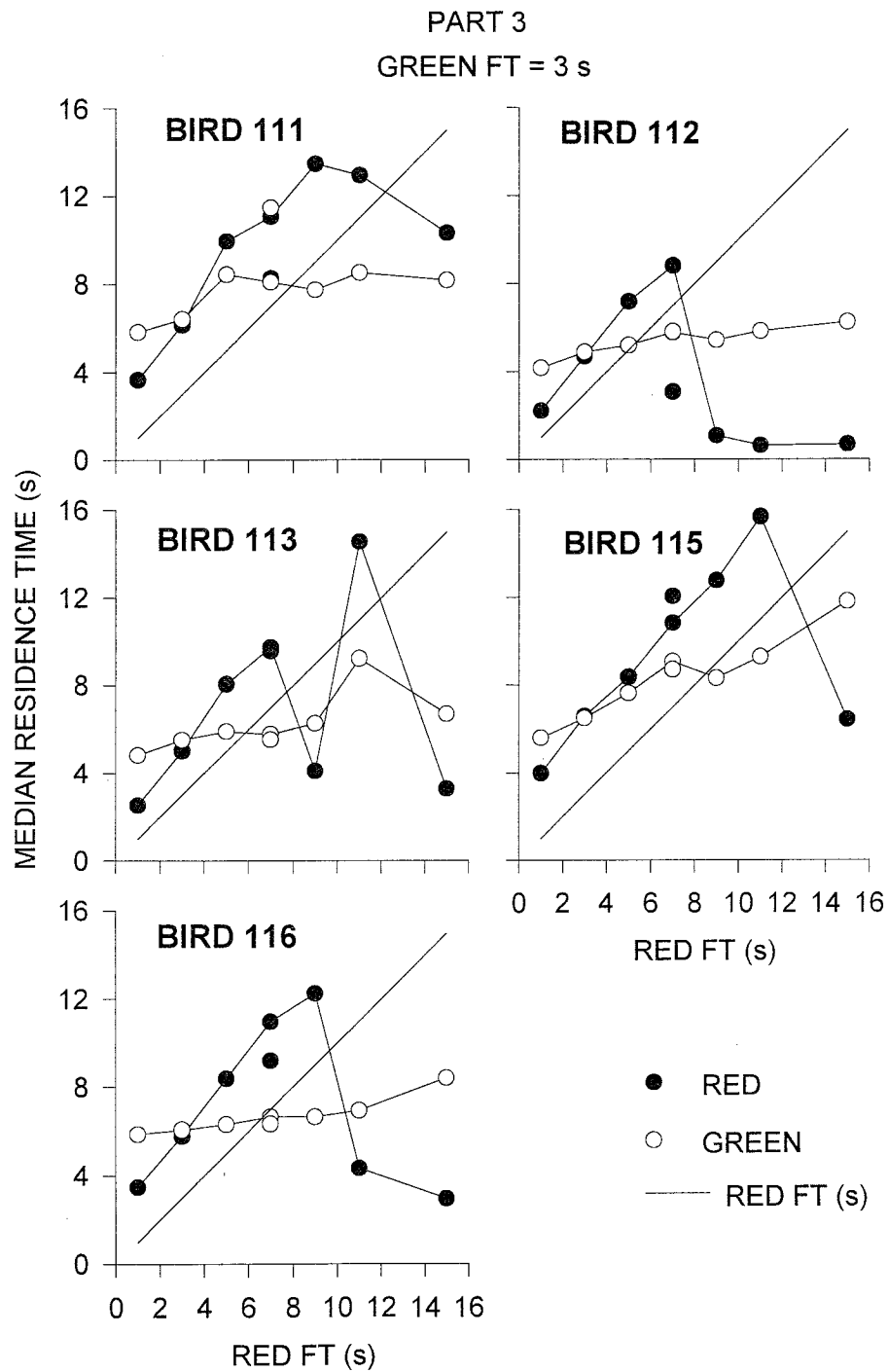
Fig. 3.   Median residence times for all 5 subjects in the red and green patches in Part 3 when the green FT arrival time was 3 s and the red arrival time was varied from 1 to 15 s. Replications are shown by unjoined points.

ever, as in Part 1, there was evidence of falling residence times for all subjects at longer arrival times. At FT 15 s, all median residence times on the red alternative were less, often considerably so, than 15 s. Figure 3 also shows that residence times in the green alternative that arranged a constant 3-s arrival time increased with increases in red arrival times for all 5 subjects, a result that is significant on a nonparametric trend test (Ferguson, 1971) at $p < .05$.

When the red arrival time was kept at 7 s and the green arrival time was varied (Figure 4), green residence times increased with green arrival time, but so also did red residence times for all 5 subjects (significant on a nonparametric trend test at $p < .05$). Unlike the results from Part 3, green median residence times did not fall below green arrival times in any condition for any subject. Replicated conditions gave data similar to original conditions.

Initial analyses showed that, consistent with the scalar property of time and scalar expectancy theory (Gibbon et al., 1988), interquartile ranges of residence-time distributions increased with increasing arrival times (see also Davison, 1996). However, these data are not shown here for reasons that will become obvious. As part of an analysis of variance in timing, we looked closely at the frequency distributions of residence times in all conditions of the experiment. Figures 5 to 8 show residence-time distributions (with a bin size of 0.5 s) for Bird 116 over all conditions of the experiment. The results for this subject were representative of those from the other subjects (see Figure 9). These figures show that in many conditions residence times were bimodally, rather than unimodally, distributed. Figure 5 (Part 1) shows that, in conditions in which two modes existed, the first mode remained at a constant residence time, whereas the location of the second mode tracked the value of the reinforcer arrival time (but was usually at a duration longer than the arrival time). Clearly, the overall median residence times shown in Figure 1 resulted both from the varying locations of the second modes and the relative frequencies of residence times comprising the first and second modes. Figure 6 (Part 2) shows the residence-time distributions when both FTs were 5 s and the probability of reinforcement in each patch

was varied. The locations of both the first and second modes appeared to remain constant across conditions, but the relative frequency of residence times associated with these two modes varied considerably. Thus, the substantial change in the median residence times in Part 2 (Figure 2) was caused mainly by changes in the relative frequencies of residence times associated with the two unchanging modes.

Figure 7, like Figure 5, shows that when the red arrival time was increased in Part 3, the location of the first mode in the distributions of residence times in the red patch remained approximately constant, whereas the location of the second mode increased and was always longer than the arrival time. Residence times in the constant green patch showed both a first and a second mode in three conditions, and the location of both modes was apparently constant (but see below). Again, therefore, the changes in median green residence times in Part 3 (Figure 3) arose largely from different frequencies of first- and second-mode residence times. Finally, when the green arrival time was varied with the red arrival time constant at 7 s (Part 4, Figure 8), the green second-mode location followed the green arrival time, with an increasing first-mode frequency as the arrival time became longer. However, in the red alternative, there seemed to be some evidence of an increasing second-mode location with increases in the green arrival time.

In general then, the locations of the shorter duration mode in the residence-time distributions appeared to remain constant, and the location of the longer duration mode varied, with the arrival time of the reinforcer in the patch. However, the relative frequencies of residence times comprising the first and second modes were systematically related to the differences between the arrival times and probabilities of reinforcers in each patch. As such differences were increased, the frequency of shorter duration mode residence times increased, and the frequency of longer duration mode residence times decreased.

We have summarized the mode-location findings for all subjects in Figure 9. The data in this figure are the estimated locations of the peaks of the first- and second-mode distributions of residence times, and these were obtained in the following way: The residence-
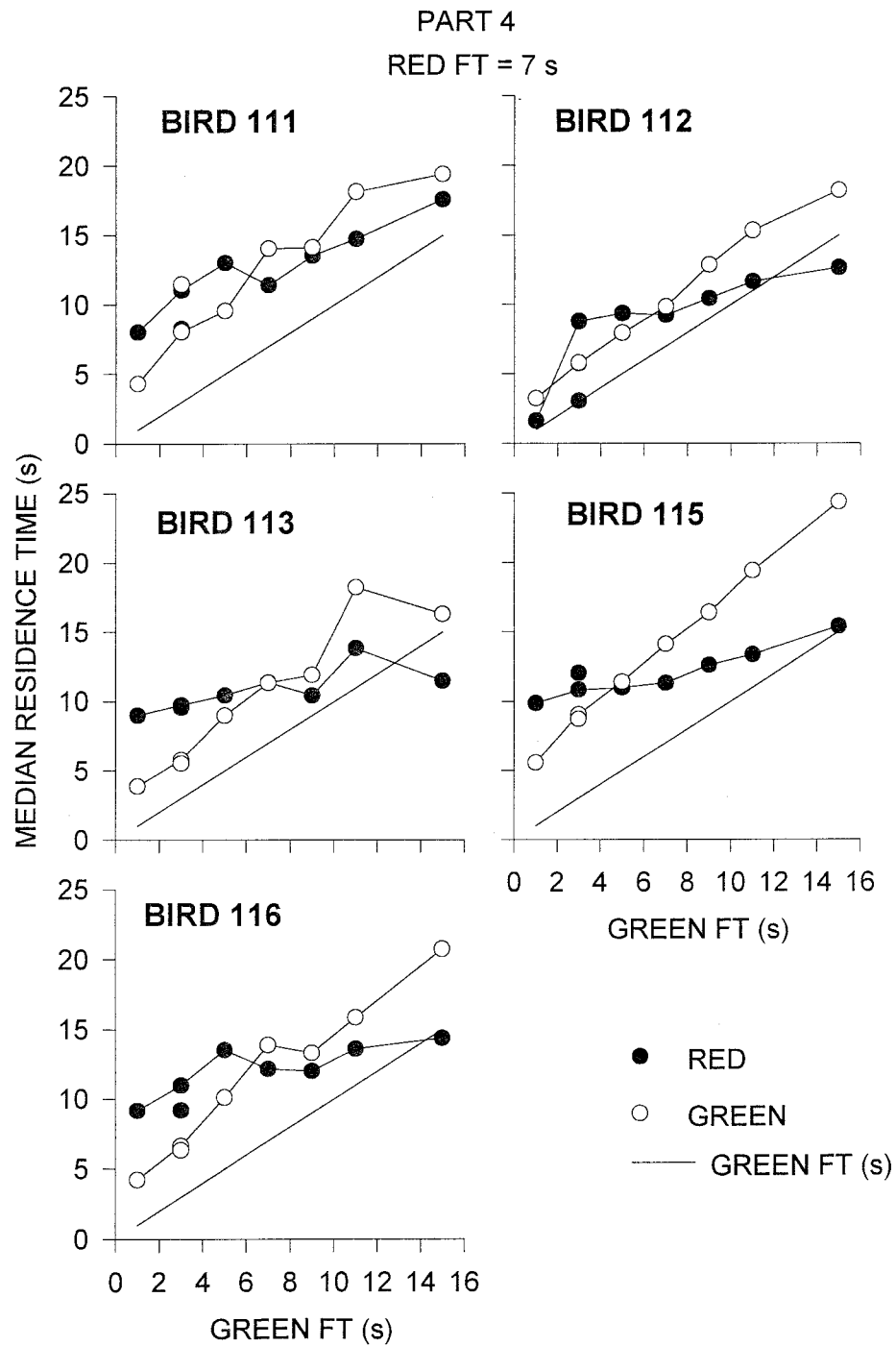
PART 4

RED FT = 7 s

Fig. 4.   Median residence times for all 5 subjects in the red and green patches in Part 4 when the red FT arrival time was 7 s and the green arrival time was varied from 1 to 15 s. Replications are shown by unjoined points.
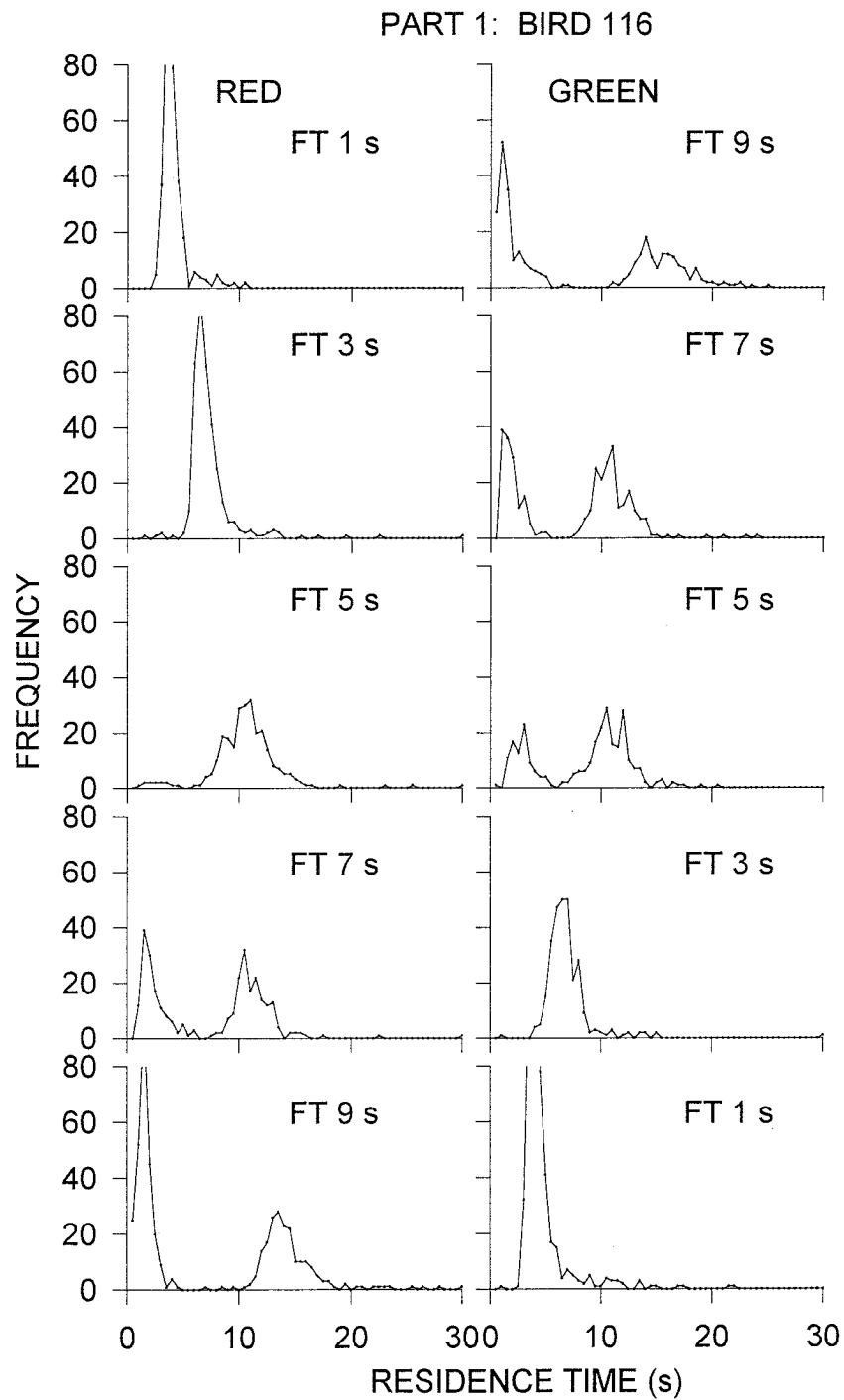
Fig. 5. Residence-time frequencies in 0.5-s bins in Part 1 (excluding replications). Red and green FT arrival times summed to 10 s, and each was varied from 1 to 9 s. The data are from Bird 116.
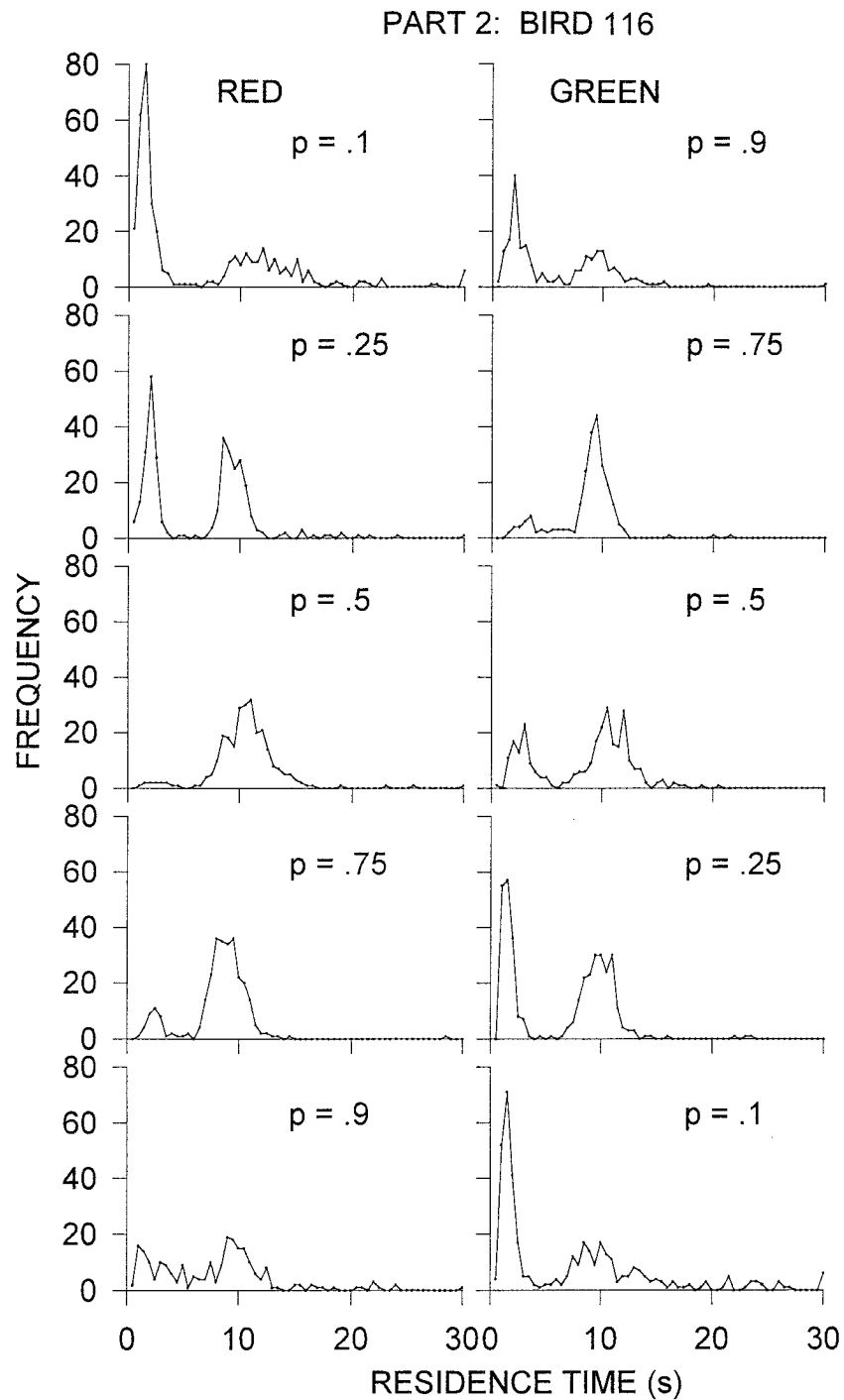
PART 2: BIRD 116

Fig. 6.   Residence-time frequencies in 0.5-s bins in Part 2. Red and green FT arrival times were both 5 s. The probability of reinforcement in the patches summed to 1.0, and each was varied from .1 to .9. The data are from Bird 116.

PART 3: BIRD 116

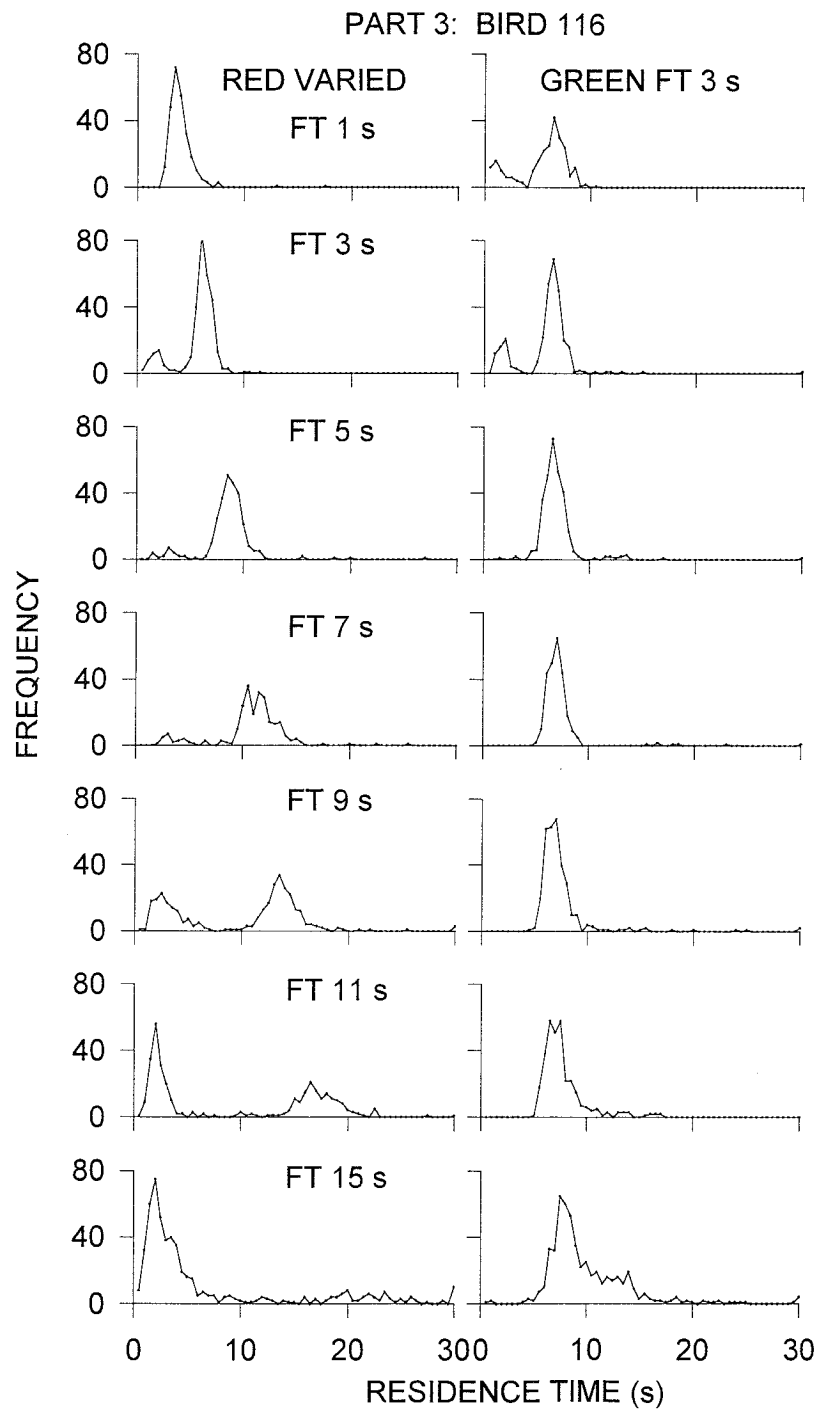Fig. 7. Residence-time frequencies in 0.5-s bins in Part 3 (excluding replications). The green FT arrival time was 3 s, and the red arrival time was varied from 1 to 15 s. The data are from Bird 116.

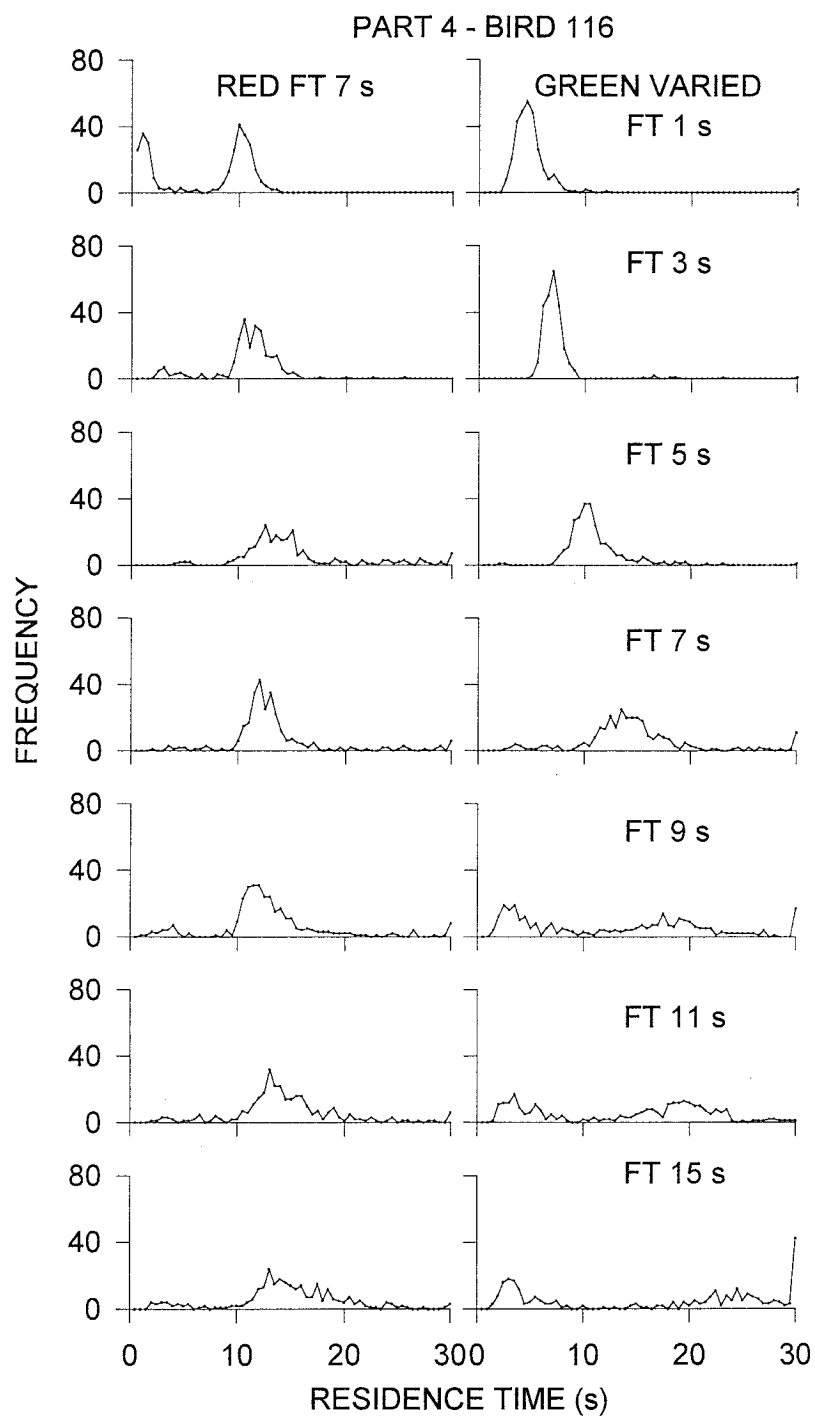Fig. 8. Residence-time frequencies in 0.5-s bins in Part 4 (excluding replications). The red FT arrival time was 7 s, and the green arrival time was varied from 1 to 15 s. The data are from Bird 116.
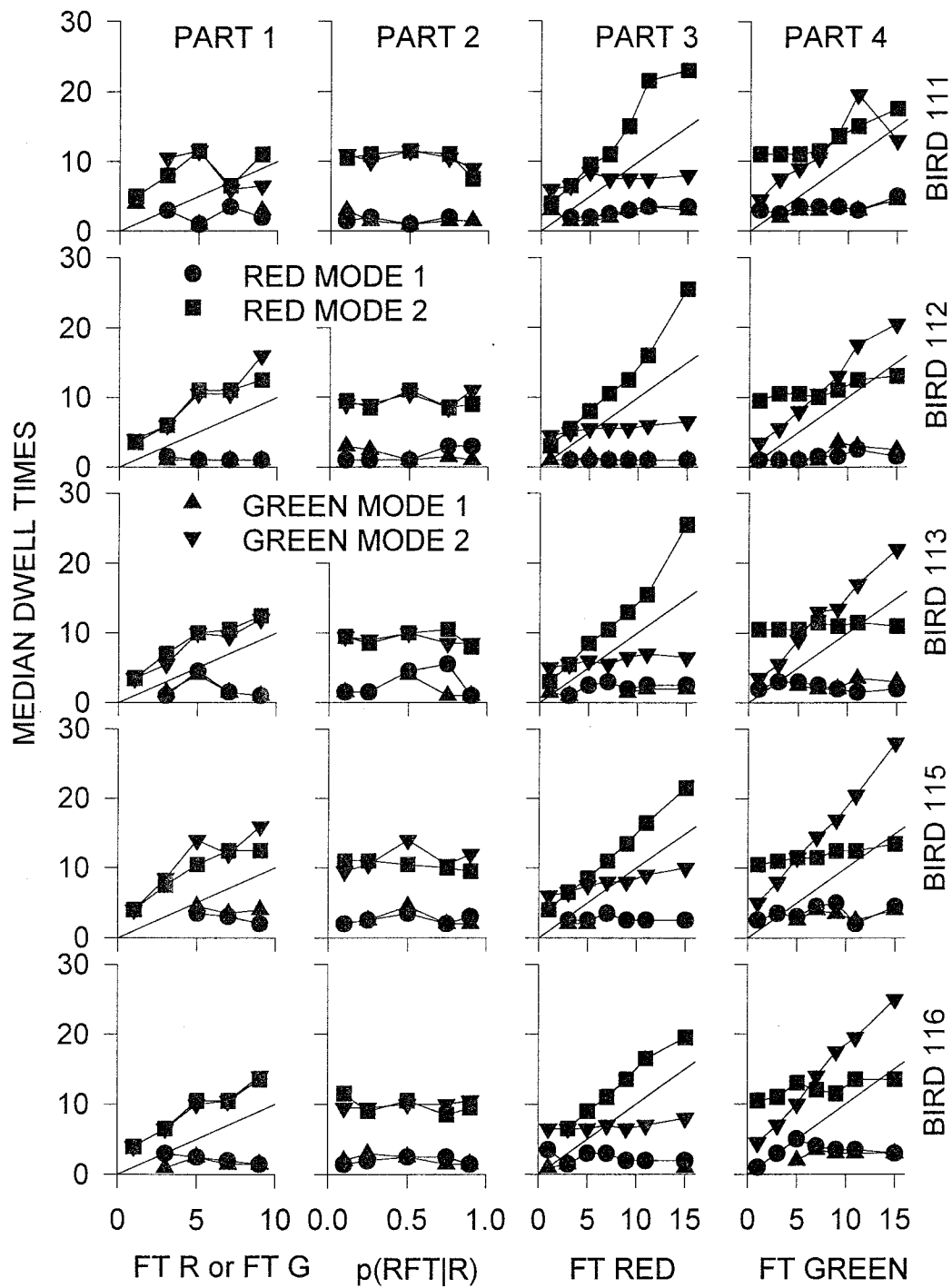
Fig. 9. The locations of the first- and second-mode residence times for each bird in the four parts of the experiment. Locations were determined by inspection of smoothed distributions (see text).

time distributions were first smoothed using a moving-average procedure (using ±1 bin), and the modes were obtained from inspecting the smoothed distributions. If two adjacent bins were the same frequency, one was chosen after inspecting the frequencies around these bins. If a peak in the smoothed residence-time distributions was not plainly evident, no mode was recorded, and if only one was evident, it was allocated to a first or second mode according to its similarity with other first and second modes. Figure 9 shows first that there was no obvious change in first-mode location in any part of the experiment, and nonparametric tests for trend (Ferguson, 1971) confirmed the lack of any significant trend. This mode was generally in the range of 1 to 3 s. All second-mode locations significantly increased (trend test, $p < .05$, two tailed) if the arrival time in that alternative increased. Finally, trend tests on the constant FT data in Parts 3 and 4 showed that these modes also increased significantly ($p < .05$) when the varied FT was changed, but it is evident from Figure 9 that the extent of this increase was very much less than the changes in the modes for the varied FT. Finally, the data from Part 2 showed that probability of reinforcement had no significant effect on either first- or second-mode locations.

DISCUSSION

In previous research in this area, the general finding has been that residence times in patches with fixed times to reinforcer arrival were longer than the arranged arrival times (Brunner et al., 1992) and longer than the longest arrival time when arrival-time distributions were arranged according to a rectangular distribution (Kamil et al., 1993). Such behavior is less than optimal if, and only if, subjects' judgments of, or memory for, times from patch entry to reinforcement arrival are precise. If they are imprecise, then, as Brunner et al. showed, optimal performance will show some degree of overstaying. It is thus reasonably simple to explain overstaying. However, it is much more difficult, at first blush, to explain why median residence times should ever be shorter than reinforcer-arrival times. Many such examples of premature exiting have been obtained in the present research.

In our introduction, we suggested that residence times shorter than arrival times may be related to large differentials in times to reinforcers between patches. When a patch stimulus that signals a long time to the next reinforcer is presented and the time to the alternative reinforcer (available via a change-over response) is shorter, even including the travel time, the values of the two delayed reinforcers (e.g., Mazur, 1984) are likely to be such that switching is more highly reinforced than is remaining in a patch, despite the dependent nature of reinforcer scheduling in this experiment. The question that we wish to raise is this: If this is so, will all residence times in the longer arrival-time patch be lessened, or will only some be lessened? This is the question that led us to look in more detail at the frequency distributions of residence times in each condition of the experiment (Figures 5 to 9).

Our interpretation of the data in Figure 9 is straightforward. The first-mode locations and frequencies of residence times at these locations are controlled by the relative values of the delayed reinforcers (e.g., Mazur, 1984) in the two patches. Residence times of animals foraging in patches such as these are at least partly controlled by reinforcers that are available in an alternative patch. When animals enter patches that signal that prey is available at times longer than those potentially available in an alternative patch, they are likely to exit that patch. Such exiting is understandable under a modification of Brunner et al.'s (1992) scalar expectancy approach: If, on patch entry, a sample of time to the reinforcer in the current patch is compared with a sample of time to the reinforcer in the alternative patch (inclusive of travel time), and the latter is shorter than the former, patch exit should occur. We suspect that the same reinforcer control, via this mechanism, occurs even in the single "some patches are empty" paradigm, although this effect may be hard to demonstrate. Kamil et al. (1993) provided little information about residence-time distributions, and it is difficult to interpret the distributions of "giving in times" (times between patch entry and the last response emitted in a patch) reported by Brunner et al. (1992) (see their Figure 5). However, some of the residence-time distributions for FT arrival times reported by Dav-

ison (1996) showed evidence of bimodality when either arrival times or travel times were short. Although it is true in the single-patch procedure that, arithmetically speaking, the alternative reinforcer is never closer in time than that potentially available in the present patch, if there is variance in the remembered times to reinforcers in patches, sampling from this distribution will certainly, on occasion, produce a result that favors immediate patch exit. Thus, mean or median residence times obtained from single-patch foraging procedures may not, as found here, be pure timing measures, but may also be controlled by differential reinforcer values for staying and exiting. Reinforcement for patch exit responses may bias residence times toward values smaller than those that would be produced by more exclusive control by time parameters, but this process may have a differential effect as a function of arrival time, and we suspect that the increased reinforcer delays (and decreased reinforcer values) would produce a reduced effect of differential reinforcement for exiting at longer arrival times. The differential reinforcement effect should certainly be decreased by longer travel times. Indeed, the effect of increasing travel time on residence time (see Davison & McCarthy, 1994; Kamil et al., 1993) could, in the light of these results, result partly from progressively decreasing premature exiting (first-mode frequencies). In addition, if short travel times (i.e., potentially short delays to food) reinforce premature switching, long travel times are likely to have the opposite effect and act as a punisher for exit responses.

The second-mode data in Figure 9 can be interpreted as unbiased, or relatively unbiased, timing measures. Second-mode residence times appeared to increase at a higher rate than their associated arrival times (Figure 9), and this timing aspect of performance is therefore consistent with predictions from scalar expectancy theory (see Brunner et al., 1992). Also consistent with the scalar property of time, the variances of the second-mode distributions generally increased with increased second-mode residence times (Figures 5 to 8). Indeed, the lack of effect in Part 2 of the probability of prey on second-mode values is entirely consistent with the scalar expectancy approach.

The present results, and much of the present interpretation, are consistent with extensive temporal differentiation results reported by Zeiler (1985). Zeiler investigated performance in concurrent random-interval (exponential variable-interval) differential-reinforcement-of-other-behavior (DRO) schedules. As found here, pause times in the DRO component were bimodally distributed, with one mode at very short pause times and another at pause times longer than the DRO requirement (see his Figure 1). He also found that the relative probability of reinforcement for the two alternatives did not affect the mean of the longer distribution (see his Figure 4, and compare our results from Part 2). Finally, the means of the second (longer) distributions increased with DRO value with a slope greater than 1 (as we found, as shown in Figure 9). Thus, two quite different procedures have provided almost identical results, and Zeiler's interpretation that the first-mode pause times have little to do with timing agrees with our interpretation. For research on timing, then, first-mode data may be irrelevant and can be discarded. However, in terms of foraging, and theories of foraging, the first-mode data are important because they do, on occasion, comprise the majority of residence times (e.g., Figures 5 to 8). In the foraging context, they require explanation.

The analysis of residence-time distributions presented above discriminates, then, between mode locations and mode frequencies. First-mode residence times are presumably *patch-rejection* responses, whereas second-mode residence times are concerned with *patch acceptance*. These results, therefore, make contact with the foraging situations investigated by Lea (1981), Abarca and Fantino (1982), and Fantino and Abarca (1985), in which the major data are concerned with acceptance and rejection of patches containing prey. The relative frequencies of residence times in the first and second modes are presumably controlled by the relative values of current-patch and alternative-patch reinforcers, and hence by times to reinforcers in patches and by travel times. At present, we suspect that travel time will affect only modal frequencies, and not modal locations, whereas arrival times will affect both modal frequencies and second-mode locations. The data from Parts 3 and 4 (Figure 9), however, fail to support at

least one aspect of this suggestion: The significant increase in the green FT 3-s and red FT 7-s second-mode residence times suggests that arrival times in the varied patch affected the alternative second-mode locations, at least to some extent. The explanation for this is unclear to us at present, but it may be that the changing overall reinforcer rates in these two parts (unlike Parts 1 and 2) affected timing accuracy. If, as in the behavioral theory of timing (Killeen & Fetterman, 1988), the pacemaker rate is dependent on the overall reinforcer rate, the timing of the unchanging fixed times to reinforcers could be affected.

In summary, the present research has shown that average residence times in patch-residence experiments comprise two components, which we interpret as an acceptance component and a rejection component. These two components are difficult to separate when arrival times are variable (Davison & McCarthy, 1994; Kamil et al., 1993; McCarthy et al., 1994) and when the reinforcer parameters of alternate patches are the same as those in the current patch. However, if remembered times to FT reinforcers are variable, and hence remembered times to variable-delay reinforcers are even more variable, then patch rejection, controlled by times to reinforcers in alternative patches that appear to be shorter than those in the current patch, will occur. To this extent, mean or median residence-time measures in such procedures will not be pure unbiased timing measures (Zeiler, 1985), but will be contaminated by reinforcer potentials in alternate patches. When the two effects were dissociated by looking at the residence-time distributions, longer residence-time modes continued to show effects, such as overstaying and rates of increase that are greater than the increase in arrival time, that are consistent with the scalar properties of timing and thus with scalar expectancy theory (Brunner et al., 1992).

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APPENDIX

Median residence times in red and green patches in each condition for each subject. The data are from the final five sessions of each condition.

	Median residence times (s)									
	Bird 111		Bird 112		Bird 113		Bird 115		Bird 116	
Condition	Red	Green	Red	Green	Red	Green	Red	Green	Red	Green
1	11.14	11.77	9.96	8.53	9.45	8.72	10.30	13.58	10.31	9.67
2	8.27	11.48	3.08	5.81	9.58	5.54	12.04	8.71	9.20	6.34
3	5.50	6.49	3.44	1.63	3.40	1.19	4.55	14.36	3.53	3.79
4	7.88	6.56	6.06	3.06	6.74	8.36	7.26	11.70	6.51	9.19
5	9.67	4.42	0.87	3.73	1.37	3.21	2.76	4.08	2.12	3.80
6	11.19	8.85	7.62	4.79	10.51	5.90	9.48	9.22	8.41	7.87
7	3.54	10.14	1.47	6.51	2.72	9.36	2.43	10.60	1.98	3.73
8	8.31	7.79	8.00	1.22	9.04	1.59	9.49	6.33	8.44	4.05
9	4.83	9.93	7.10	8.51	7.46	8.83	9.49	10.45	8.00	8.95
10	9.94	8.43	7.17	5.20	8.07	5.91	8.36	7.63	8.39	6.32
11	8.03	4.31	1.64	3.25	9.00	3.89	9.86	5.58	9.18	4.23
12	6.15	6.41	4.70	4.90	5.01	5.52	6.58	6.49	5.79	6.07
13	13.54	14.13	10.47	12.86	10.43	11.92	12.62	16.42	12.01	13.31
14	11.07	8.08	8.81	5.78	9.75	5.78	10.82	9.06	10.98	6.64
15	3.66	5.82	2.22	4.17	2.54	4.83	3.98	5.59	3.48	5.86
16	11.41	14.05	9.24	9.85	11.38	11.34	11.32	14.12	12.17	13.89
17	13.47	7.73	1.07	5.43	4.11	6.28	12.76	8.31	12.25	6.64
18	13.03	9.57	9.38	7.96	10.44	8.99	10.98	11.41	13.52	10.12
19	14.76	18.15	11.66	15.34	13.85	18.24	13.38	19.42	13.62	15.87
20	12.94	8.51	0.63	5.84	14.57	9.23	15.68	9.28	4.34	6.94
21	17.60	19.41	12.65	18.23	11.49	16.31	15.41	24.36	14.37	20.74
22	10.32	8.16	0.68	6.25	3.29	6.70	6.43	11.82	2.96	8.40